INTERFERENCE AND EXPLOITATION IN BIRD COMMUNITIES

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The past two decades of research on the population ecology of birds have produced a great deal of activity and controversy in relation to the role of competition in determining which species can live together in the same habitat (Wiens 1977, Diamond 1978, Schoener 1982). It has long been realized that there are at least two ways in which competition between species can occur (Miller 1967, Morse 1980a). The first is commonly called exploitative competition and involves the removal of resources by one species, leaving less for competing species. The second type of competition, termed interference, includes processes by which the activities of one species prevent the use of resources by other species. Authors of nearly every study of competition in bird communities have either assumed that all types of competition lead to the same ecological and evolutionary consequences or that competition involves only exploitation.

Recent published research on competition has been based almost exclusively on the Lotka-Volterra paradigm of population growth (MacArthur 1972). MacArthur (1958), following the early insights of Lack (see Lack 1971), was one of the first researchers to bring a body of earlier mathematical arguments (e.g., Lotka 1925, Gause 1934) to bear on the problem of species coexistence in relatively uniform habitats. MacArthur's (1958) point was that each of the birds in the community he studied had features related to their foraging activities which prevented them from using exactly the same resources, and hence they could live in the same community. A number of subsequent studies (e.g., Cody 1974, Schoener 1974) attempted to extend and verify MacArthur's (1972) ideas, summarized in his book.

This attention to competition as a mechanism of "structuring" bird communities, and communities in general, led to a growing consensus regarding the mechanisms that regulated the distribution and abundance of organisms (Cody and Diamond 1975). However, Wiens (1976, 1977) posed important questions regarding the developing theory of community structure. He suggested that the environments in which bird communities existed varied much more than was commonly recognized by community theory. Though Fretwell (1972) had made attempts to incorporate environmental variability due to seasonality into the theory, Wiens (1977) implied that the problem was too serious to be incorporated into the existing theory. Responses to Wiens' criticisms by influential ecologists

(Diamond 1978, Cody 1981, Schoener 1982), though appealing, have not been convincing. Currently, many authors studying a variety of bird communities are equally divided in the interpretation of their results (e.g., Cody 1978; Wiens and Rotenberry 1979, 1980, 1981a, b; Rotenberry and Wiens 1980a, b; Noon 1981; Rusterholz 1981; Collins et al. 1982; Nudds 1982; Rosenberg et al. 1982; Toft et al. 1982).

In the following paragraphs, I suggest that a great deal of the present confusion has been derived from a mistaken impression, due to use of the Lotka-Volterra competition model, that the ecological and evolutionary results of exploitative competition and interference competition are the same. While conceptualizing and rigorously defining the ecological consequences of these differing competitive processes may not provide a unifying basis for explaining why bird species occur in the combinations they do in the natural world, I believe it is important that ideas be as clearly defined as possible in order to facilitate the formation of adequate hypotheses. The formulation and testing of rigorous hypotheses for local species assemblages promises to be more fruitful for the progress of avian ecology than a new generation of complex, abstract mathematical models (Pielou 1981, Simberloff 1982).

THE CONVENTIONAL PARADIGM

Both the proponents and antagonists of competition theory view competition from the perspective of the Lotka-Volterra model. The appeal of the logistic model to ecology today has partly resulted from interesting interactions among early twentieth century ecologists who passed on an academic tradition to ecologists in the 1950's and 1960's (Kingsland 1982), however, it is also conceptually simple. To apply the logistic model to real species assemblages, however, at least two assumptions about the species assemblages are needed. The first is that the resources available to the species are limited. Here resources are most commonly assumed to be food resources, and thus the competitive mechanism is exploitation. However, if the resource being considered is space, then interference might be envisioned as the mechanism of competition. A second assumption is that the population densities of the species are near equilibrium (i.e., $N_i \cong K_i$). These two assumptions ensure that changes in population densities of the species will be dominated by the competition coefficients. To see this, assume in the logistic equation for species i

$$\frac{dN_i}{dt} = \frac{r_i N_i}{K_i}\left(K_i - N_i - \sum_{j \neq i} \alpha_{ji} N_j\right),$$

that $N_i \cong K_i$, then $N_i/K_i \cong 1$ and $K_i - N_i \cong 0$, so

$$\frac{dN_i}{dt} \cong -r_i \sum_{j \neq i} \alpha_{ji} N_j.$$

One major result that follows from the Lotka-Volterra equations is that when resources (however defined) are abundant, species carrying capacities (K_i) are much larger than their population sizes, and hence the term ($-N_i - \sum_{j \neq i} \alpha_{ji} N_j$) is small compared to K_i. In such situations the effects of competition are thought to be relaxed (Fretwell 1972).

It is obvious from an examination of Wiens' (1977) criticisms of competition theory that he envisioned essentially the same type of competitive model as suggested above. His ecological crunch model rested on the assumption that as resources become more abundant competition relaxes and coexistence of species is facilitated, which is essentially an extension of Fretwell's (1972) analysis to include seasons in which resource abundance varies widely.

INTERFERENCE AND EXPLOITATIVE COMPETITION

In his discussion of the mechanisms of competition, Schoener (1983) subdivided the two general categories of exploitation and interference into several categories. His first category, termed "consumptive" competition, refers to what most researchers generally term exploitative competition. This process involves removal of resources by one species leaving less for competing species. Schoener (1983) divided interference competition into a number of categories, three of which are applicable to avian species. The first type, which he termed "preemptive" occurs when an individual occupies a unit of space in which some needed resource exists, and simply by its presence interferes with the ability of another individual of a competing species to use the resource contained in that space. Schoener (1983) pointed out that this primarily involved sessile organisms, but this type of competition may also apply to organisms which require a fixed unit space, e.g., nest-sites in birds. In the discussion below, this type of competition will not be considered. The second type of interference which Schoener (1983) recognized was termed "territorial" competition, a process whereby an individual of a competing species aggressively defends a unit of space in some manner against individuals of another species. Finally, Schoener (1983) recognized that mobile individuals of different species, while in the course of their movements in a habitat, might cause some sort of stress or injury on each other. He termed this type of competition "encounter" competition. Encounter competition may occur as an active behavioral adjustment by individuals of competing species to prevent resource acquisition or population growth of competitors, leading

to reduced resource intake or loss of individuals. This type of interference may be termed active interference. Encounter competition as Schoener (1983) defined it may also occur as the consequence of nonaggressive behaviors. This type of interference competition might be termed passive interference. Charnov et al. (1976) first recognized that this type of interference might be important in structuring communities. They suggested that the foraging activities of some species which consume mobile prey might result in movements of prey into "refugia" where they are unavailable to competitors. Hence, resources would be temporarily depressed, rather than depleted as might occur from consumptive competition. Passive interference might also occur between individuals of different species whose foraging paths cross close enough in space and time so that the foraging activities of one or both individuals is impeded or prevented exclusive of any antagonistic responses.

Exploitation and interference competition are likely to be prominent in different ecological settings. Active forms of interference necessarily carry with them costs (Case and Gilpin 1974, Schoener 1976) which place constraints on the abilities of species to actively interfere. Hence, resources must be abundant enough to offset the costs of active interference. Morse (1980a) also points out that resources should be predictable in space and time in order for interference to confer benefits on individuals. Passive interference, on the other hand, is likely to occur any time resources become concentrated. Birds often respond to increased productivity by increasing population densities (Dunning and Brown 1982). Increased population densities should lead to greater likelihood of individuals of competing species encountering each other and thus increase the frequency of passive interference events.

Based on these ideas a tentative model of the ecological settings in which each type of competition should occur can be constructed (Table 1). The applicability of this model is based on the assumption that resources (however defined) are the primary factors to which the species respond on an evolutionary time scale. Hence, if patterns in the physical environment that are independent of resource characteristics (e.g., temperature as it effects thermoregulation) are more important than resources in shaping the species' behavior, then the model discussed below may only poorly fit the actual behavior of the species. Species should respond to three characteristics of resources. First, resource density should affect competitive behavior between species since active interference has costs in terms of energy expenditure associated with it. It is assumed that an individual cannot gather resources and actively interfere with another individual at the same time, hence active interference is more likely to occur when an individual can quickly replenish its energy stores. Second,

TABLE 1

TYPES OF INTERSPECIFIC COMPETITION WHICH MAY BE OBSERVED IN DIFFERENT
ECOLOGICAL SETTINGS; THE ENTRIES ARE THE TYPE OF COMPETITION MOST LIKELY TO BE
ASSOCIATED WITH THE ECOLOGICAL SETTING DESCRIBED

Resource density	Resource dispersion	Temporal patterns of resource abundance	
		Predictable	Unpredictable
Abundant	Concentrated	Active and passive interference, territoriality	Passive interference, facultative active interference
Abundant	Dispersed	Passive interference facultative active interference	Exploitation
Rare	Concentrated	Active and passive interference, territoriality (rarely)	Passive interference, facultative active interference
Rare	Dispersed	Exploitation	Exploitation

the spatial patterning of resources should influence the ability of species to defend resources successfully. Resources which are concentrated in small areas require less energy expenditure to defend, and hence are more likely to allow species to maintain small enough cost-benefit ratios to make active interference feasible. Finally, the temporal patterning of resource abundance should influence the ability of species to develop resource defense systems. If resources are highly stochastic in their appearance, then individuals should not be able to gain enough benefit on a regular basis to allow them to be successful at resource defense (Morse 1980a). On the other hand, resources that are regular on an ecological time scale should be used by more species than those that are sporadic, hence increasing opportunities for individuals to develop behavioral mechanisms of dealing with interspecific competitors. It should be obvious that these three characteristics of resources interact and provide a number of different ecological settings in which interspecific competitive mechanisms might evolve (Table 1).

When resources are abundant, concentrated and predictable active interference is feasible (Table 1) since individuals can expend relatively little energy on resource defense and rapidly obtain necessary energy to replace energy spent. In such an ecological setting, it would be advantageous for species to develop territorial or hierarchical systems whereby interspecific contests are settled quickly with a minimum of energy expenditure. However, when resources are abundant and concentrated, but

appear sporadically and unpredictably, the benefits an organism may derive from them may not be regular enough over time to allow species to invest the energy necessary to maintain resource defense. In such a setting, during periods of irregular resource abundance, individuals might benefit from maintaining a behavioral flexibility (facultative active interference in Table 1) enabling them to actively interfere during times of resource abundance, and cease interference during times of resource rarity. If resources are abundant, and predictable, yet dispersed enough so that energy costs for defending more than a single resource unit are high, then again it would be advantageous for an individual to actively interfere with another only sporadically. In such a setting, passive interference events might occur on a regular basis since densities would be high. If resources are abundant and dispersed, but unpredictable, then densities of consumers might remain low during irregular resource pulses, and consumptive competition might exist only during the periods of low resource density (see below).

When resources are rare, it will be more difficult for individuals to invest in behaviors which involve elaborate energy expenditures, hence active interference may be less prevalent in habitats with scarce resources than in habitats with resource abundance. When resources are concentrated in such habitats, the resulting ecological conditions might give rise to qualitatively similar patterns of interspecific competitive mechanisms to those found when resources are abundant, but less expensive forms of interference might be expected and interspecific territoriality should be relatively rare. When resources are rare and dispersed, then individuals might only be able to expend energy on resource acquisition (e.g., foraging). Hence the only way species might compete in such situations might be to remove the already limited supply of resources from the area of joint occupancy of two competing species.

It should be realized that testing the predictions of the model described above might be very difficult. While the model has been constructed in a dichotomous fashion, terms such as "rare" and "abundant" are likely to represent extremes along a continuum of resource abundances. To test even the qualitative predictions of the model it would be necessary to generate more precise definitions of the nature of resource density, dispersion, and temporal patterning based on a specific system. Another complicating factor is that environments in which species exist are not constant but usually change in a cyclic or stochastic manner. Hence, at a given time, a habitat might present a setting in which resources are abundant, concentrated, and predictable and later that same habitat might have rare resources that are dispersed and unpredictable. In the following section, I review a number of studies that deal with avian competition in

the context of the model presented above, however, the level of rigor of these studies does not allow a rigorous evaluation of the usefulness of the model in predicting the types of competitive interactions that species might experience.

COMPETITION IN BIRD COMMUNITIES

What is the prevalence of interference and exploitation in bird communities and to what extent do they shape ecological relationships among bird species? To adequately answer these questions one would need a large number of studies on many species assemblages done at a level of rigor sufficient to differentiate among the intensity of the types of competition envisioned in the model discussed in the preceding section. Such a sample is probably impossible to obtain, however, a number of studies have been done which provide at least a rough idea of the nature and prevalence of the several types of competition in real ecosystems.

Some studies have suggested that since aggressive encounters were infrequently observed among species, the major mode of the presumed competition among the species studied was exploitation (Noon 1981, Rusterholz 1981). From the preceding discussion, however, it follows that absence of active interference events does not indicate absence of all interference interactions. At this time it is extremely difficult to document the presence and frequency of passive interference events. Such events are very likely to go undetected by human observers because they do not create sufficient auditory or visual cues to attract attention.

Because the mechanism of exploitation depends on the ability of one species to reduce prey numbers to a level that would have a significant impact on the population growth rate of other species, studies which demonstrate a drop in prey numbers attributable to avian predation are extremely important in assessing the probability of exploitation being an important factor influencing bird communities. A number of studies have provided both direct and indirect evidence for the ability of birds to reduce prey numbers. Both Solomon and Glen (1979) and Holmes et al. (1979) performed experiments in which avian predators were prevented from removing prey in certain areas. Both studies demonstrated a measurable increase in prey in areas not available to avian predators. Recently, E. O. Garton (pers. comm.) has found similar results for birds preying on the western spruce budworm (*Choristoneura fumiferana*). Gunnarson (1983) showed that overwinter mortality of spiders living in spruce trees was lower on branches on which netting had been used to prevent avian predation. Similar results were obtained by Askenmo et al. (1977) in another investigation of the impact of wintering birds on spiders in spruce forests. Hence, experimental evidence suggests that avian predation can

cause significant reductions in arthropod densities during both the breeding and nonbreeding seasons. In a slightly different vein Gill and Wolf (1979) showed that sunbirds (*Nectarinia* spp.) could remove significant amounts of nectar potentially available to other species.

A number of studies have provided indirect support of the role of avian predators in reducing population densities of their prey. Gibb (1954) noted that Great Tits (*Parus major*) apparently reduced insect larvae to a certain specific level before moving to feed elsewhere. Peterman et al. (1979) reviewed studies on the eastern spruce budworm which suggested that avian predators played an important part in damping budworm irruptions. Similar evidence along these lines was reviewed by Otvos (1979). Heinrich (1979) discovered that lepidopteran larvae palatable to birds tended to forage in a manner which minimized the visual impact of their foraging activities. Many of these larvae are also cryptically colored, suggesting that predators which use visual clues while hunting have been important in shaping their phenotypic characteristics.

Although evidence suggests that there is certainly potential for exploitative competition in many avian communities, most studies have failed to demonstrate that avian species could remove enough prey to affect the growth rate of other species (Maurer 1983a). This is critical information because it is possible that measurable reductions in food supply may not be sufficient to reduce the effective food supply available to a second species (Maurer 1983b). Reduced resources is a necessary, but not a sufficient condition for the occurrence of exploitative competition. Minot (1981) removed Blue Tit (*Parus caeruleus*) broods from an oak wood in England and learned that nestling weights of Great Tits were higher in the experimental area than in a control area. Since weight of nestlings is related to survival probability (Perrins 1965) this implies that Blue Tits were able to remove enough insect larvae for their broods to affect the demographics of Great Tits. In this situation, it is difficult to objectively determine the characteristics of the resources available to tits during the breeding season. It is likely that they are abundant relative to winter food availability (Gibb 1960). The insect prey of tits may be relatively evenly dispersed (Tinbergen 1960), and apparently appear at widely differing times from year to year (Tinbergen 1960, Perrins 1965). Hence, food for tits during the breeding season may be abundant, dispersed, and unpredictable.

Abundant evidence exists for the prevalence of active interference, though this may be due to the relative ease with which these types of interactions may be observed. Williams and Batzli (1979a, b) found that the presence of Red-headed Woodpeckers (*Melanerpes erythrocephalus*) influenced the distribution and foraging behavior of other bark foraging

birds during winter in central Illinois. These interactions between *M. erythrocephalus* and other bark foragers apparently relaxed during the breeding season, a time when resources presumably would be more abundant. During the winter, however, the primary foods of these species may be concentrated enough to increase the frequency of interspecific encounters over that encountered during the breeding season. Williams and Batzli (1979b) commented that the majority of aggressive encounters occurred in fall, when Red-headed Woodpeckers were establishing winter territories. Interspecific territoriality during the breeding season has been documented for a number of passerine birds (Orians and Willson 1964), including Palearctic sylviine warblers (*Sylvia* spp.) (Cody and Walter 1976, Cody 1978, Garcia 1983); (*Phylloscopus* spp.) (Saether 1983a, b) and vireos (*Vireo* spp.) (Rice 1978, Robinson 1981).

Aggressive encounters among species are not necessarily territorial conflicts (Davies 1978). Edington and Edington (1983) described several instances of active interference among West African birds. They found that in interactions among several species of sunbirds, species dominant in aggressive encounters were those for which the interaction took place in a favored feeding zone. Edington and Edington (1983) found a similar type of interaction occurred between White-throated Bee-eaters (*Merops albicollis*) and Ethiopian Swallows (*Hirundo aethiopica*). Sherry (1979) found that American Redstarts (*Setophaga ruticilla*) and Least Flycatchers (*Empidonax minimus*) interacted aggressively during the breeding season in New Hampshire although their breeding territories overlapped extensively. Morse (1976) showed that during the breeding season wood warblers (*Dendroica* spp.) in spruce forests were interspecifically aggressive, and that encounters were usually more frequent later in the season when feeding of nestlings by parents might result in many interference events during foraging. These encounters apparently did not lead to interspecific territoriality.

In assemblages of nectar-feeding birds, interesting comparisons can be made between the frequency of interference events and the qualitative predictions of the model discussed above, since the dispersion and density of the resources (nectar) can easily be measured and compared to inference behaviors. Carpenter (1978) summarized results from several nectarivore communities she studied. In a community of Hawaiian drapanidines, Carpenter (1978) showed that during a year of overall depressed nectar availability, aggression among three species of honeycreepers was increased. In the year of depressed nectar availability, flowers produced the same amount of nectar but were depleted quickly. However, flowers were concentrated in one portion of the canopy during the poor year, while they were dispersed during two favorable years. In the poor year,

all three honeycreeper species attempted to forage in the same area. The dominant species was able to defend territories in the densest flower clumps, and nectar availability in these clumps was in excess of the species requirements for maintenance. Nectar production was apparently relatively predictable within a given year, but during good years was abundant and dispersed, hence leading to few opportunities for interference. During the bad year, nectar was generally rare, but concentrated, which led to a concentration of consumers. This in turn made it necessary for two of the honeycreepers to become territorial, for otherwise they could not adequately meet their energy requirements (Carpenter 1978:810).

In a community of Australian honeyeaters (Melaphagidae), Carpenter (1978) noted that nectar was extremely abundant and that the honeyeaters in that community were not aggressive. Apparently, nectar producing flowers were not concentrated enough relative to their abundance to necessitate aggression, though aggression among honeyeaters has been reported. These species of honeyeaters, however, relied heavily on insect densities, hence the importance of nectar to their behavior is questionable. Dow (1977) showed that another melaphagid excluded all other bird species from habitat near colonies. This species was more successful in driving out other species in structurally simple habitats, where food resources could be expected to be concentrated relative to habitats with many vegetation layers.

Pimm (1978) performed an experiment with hummingbirds at feeders at which he varied the predictability of resources while keeping their density and dispersion constant. He calculated two measures of competition, one which he termed exploitation, the other which he termed interference. However, resource abundance remained constant in the experiment, and the measure of exploitation, a regression coefficient of the time that one species spent at each feeder vs the time that other species spent at each feeder (feeders were replications) was actually a measure of passive interference, since feeders were constantly replenished. His interference measure was a regression coefficient of feeder use by one species vs time spent in feeder defense in a second species, which is a measure of active interference. His results are consistent with the model presented above: a decrease in resource predictability significantly decreased both passive and active interference.

IMPLICATIONS FOR COMPETITION THEORY

Many discussions of competition implicitly assume that the effects of the different types of competition tend to produce similar results (e.g., Miller 1967). Thus, "niche partitioning," the differential use of resources by species, is assumed to have been the result of competition for limiting

resources (e.g., MacArthur 1958, Morse 1980b, Noon 1981, Alatalo 1982) regardless of the type of competition involved. This assumption is also implicit in Wiens' (1977) criticisms of competition theory. He listed several assumptions made by competition theorists in applying the theory to natural systems, many of which are artifacts of the Lotka-Volterra paradigm. For example, the assumption that resources are limiting is crucial to Lotka-Volterra competition. Wiens (1977) pointed out that very often species may exist in environments which are seasonally highly productive, and hence species densities would be far below environmental carrying capacity as envisioned in the Lotka-Volterra model (see also Fretwell 1972). Wiens (1977) assumed that in these situations, competition would generally be relaxed. However, the model presented in the present paper suggests that when resources are abundant, although exploitation is relaxed, interference may increase, especially if resource abundance is concentrated, or if species are able to respond to increased resource abundance by increasing their densities.

Some models of interference and exploitative competition have suggested that at high resource levels interference should be minimal and should increase when resources become scarce (Gill 1974, Carpenter and MacMillen 1976, Wolf 1978). However, few of these models have differentiated between resource abundance and resource dispersion. If resources become concentrated during periods of low resource levels, then interference is likely to increase because individuals must search for and secure resources in a much smaller area, hence increasing the rate of encounters with other individuals while at the same time removing a greater proportion of the resources. At high resource densities, if resources are generally dispersed then the opportunities for interference might be relaxed. The utility of the model discussed in this paper is that it considers not only variation in resource abundance, but also the spatial and temporal patterns of resource availability that may influence competitive relationships. In doing so it generalizes the model of Orians and Willson (1964), who suggested that interspecific territoriality should be more prevalent in structurally simple habitats. They felt that interspecific territoriality in such habitats should increase because fewer niches are available. The model I have presented suggests that if fewer niches exist in simple habitats, it is because resources are spatially compressed or concentrated.

Just as exploitative and interference competition might be expected in different ecological settings, the evolutionary results of these types of competition might be expected to be different. If it is assumed that reduction in competition will increase an individual's fitness, then it follows that species should evolve to reduce competition. Selection to reduce interference competition should involve different phenotypic traits than

those that are involved in exploitative competition. When the latter type of competition is occurring, resources may often be dispersed so as to be non-defendable (Table 1). If resources are rare enough, then individuals which avoid areas containing resources may be selected against. If at the same time densities of competitors are low, and hence interspecific encounter rates low, then it would be most advantageous for an individual to use all areas within its foraging range. Selection might operate in this situation to cause species to diverge in the types of resources taken so species would use different types of resources, but use all available resource patches. On the other hand, the avoidance of individuals which are likely to actively or passively interfere would reduce interference competition. Such interference would be reduced if different species used spatially (or temporally) different parts of the habitat. Hence, exploitation should generally lead to niche partitioning via reduced resource overlap while interference should lead to niche partitioning via reduced spatial overlap. For example, differences in prey size used may result from exploitation, while differences in foraging zones may result from interference.

Although the two types of competition may have different evolutionary consequences, it is likely that species evolve in highly complex environments in which both types of competition may be experienced along with numerous other factors affecting individual fitness. Hence the phenotypic results of the two types of competition may be difficult to distinguish from those produced by other selective pressures. As an example, Blue and Great tits compete for nest holes by interference (Alatalo 1982) and also have been shown to compete exploitatively for food for nestlings (Minot 1981, Alatalo 1982). The result of this array of selection pressures is that species might be constrained in their abilities to evolve to alleviate competitive pressures (Maurer, unpubl.). Though we may be able to understand general relationships among competitive pressures and niche characteristics, assigning specific selection pressures (e.g., exploitation or interference) to specific phenotypic characteristics (e.g., specific niche differences) may, in practice, be an exercise in futility because cause-effect relationships may be impossible to verify, even indirectly (Wiens and Rotenberry 1981b, Wiens 1982). Competition, whether exploitative or interference, is likely to be one of many factors which together operate on avian assemblages to shape the composition and densities of the species which comprise them.

SUMMARY

Two types of competitive interactions occur among species in bird communities: exploitation and interference. Most theoretical and empirical approaches to the ecology of competition have assumed the evolutionary and ecological results of these two processes are the

same. Interference can be active, a result of direct behavioral interactions which carry with them a cost, or passive, the indirect result of other activities of competitors (such as food gathering). A model is presented which suggests the type of ecological settings in which the various types of competition can occur. Generally, the model suggests that as resources become less abundant, more widely dispersed, and less predictable, exploitation should become more prevalent while interference should become less prevalent.

Research on birds indicates that active interference is very common, however, exploitation and passive interference, if prevalent, may be difficult to document. Discussions of the prevalence of competition have centered on the Lotka-Volterra conceptualization of competition. However, if interference is common when resources are abundant, then resource limitation may not be a prerequisite of niche divergence. Exploitation should lead to niche partitioning via reduced resource overlap, while interference should lead to niche partitioning via reduced spatial overlap. However, both of these factors may act as selection pressures on competing species in addition to many other selection pressures, hence the ability of species to respond to selection to reduce competition might be greatly modified or inhibited.

LITERATURE CITED

ALATALO, R. V. 1982. Evidence for interspecific competition among European Tits *Parus* spp.: a review. Ann. Zool. Fenn. 19:309–317.

ASKENMO, C., A. VON BRÖMSSEN, J. EKMAN, AND C. JANSSON. 1977. Impact of some wintering birds on spider abundance in spruce. Oikos 28:90–94.

CASE, T. J. AND M. E. GILPIN. 1974. Interference competition and niche theory. Proc. Natl. Acad. Sci. USA 71:3073–3077.

CARPENTER, F. L. 1978. A spectrum of nectar-eater communities. Am. Zool. 18:809–819.

——— AND R. E. MACMILLEN. 1976. Threshold model of feeding territoriality and test with a Hawaiian honeyeater. Science 194:639–642.

CHARNOV, E. L., G. H. ORIANS, AND K. HYATT. 1976. Ecological implications of resource depression. Am. Nat. 110:247–259.

CODY, M. L. 1974. Competition and the structure of bird communities. Princeton Univ. Press, Princeton, New Jersey.

———. 1978. Habitat selection and interspecific interactions among sylviid warblers in England and Sweden. Ecol. Monogr. 48:351–396.

———. 1981. Habitat selection in birds: the roles of vegetation structure, competitors, and productivity. BioScience 31:107–113.

——— AND J. M. DIAMOND. 1975. Ecology and evolution of communities. Harvard Univ. Press, Cambridge, Massachusetts.

——— AND H. WALTER. 1976. Habitat selection and interspecific interactions among Mediterranean sylviid warblers. Oikos 27:210–238.

COLLINS, S. L., F. C. JAMES, AND P. G. RISSER. 1982. Habitat relationships of wood warblers (Parulidae) in northern central Minnesota. Oikos 39:50–58.

DAVIES, N. B. 1978. Ecological questions about territorial behavior. Pp. 317–350 *in* Behavioral ecology, an evolutionary approach (J. R. Krebs and N. B. Davies, eds.). Blackwell Scientific Publications, Oxford, England.

DIAMOND, J. M. 1978. Niche shifts and the rediscovery of interspecific competition. Am. Sci. 66:322–331.

Dow, D. D. 1977. Indiscriminant interspecific aggression leading to almost sole occupancy of space by a single species of bird. Emu 77:115–121.

Dunning, J. B., Jr., and J. H. Brown. 1982. Summer rainfall and winter sparrow densities: a test of the food limitation hypothesis. Auk 99:123–129.

Edington, J. M. and M. A. Edington. 1983. Habitat partitioning and antagonistic behaviour amongst the birds of a West African scrub and plantation plot. Ibis 125:74–89.

Fretwell, S. D. 1972. Populations in a seasonal environment. Princeton Univ. Press, Princeton, New Jersey.

Garcia, E. F. J. 1983. An experimental test of competition for space between Blackcaps, *Sylvia atricapilla* and Garden Warblers, *Sylvia borin* in the breeding season. J. Anim. Ecol. 52:795–805.

Gause, F. G. 1934. The struggle for existence. Williams and Wilkins, Baltimore, Maryland.

Gibb, J. 1954. Feeding ecology of tits, with notes on Treecreeper and Goldcrest. Ibis 96:513–543.

———. 1960. Populations of tits and Goldcrests and their food supply in pine plantations. Ibis 102:163–208.

Gill, D. E. 1974. Intrinsic rate of increase, saturation density, and competitive ability. II. The evolution of competitive ability. Am. Nat. 108:103–116.

Gill, F. B. and L. L. Wolf. 1979. Nectar loss by Golden-winged Sunbirds to competitors. Auk 96:448–461.

Gunnarsson, B. 1983. Winter mortality of spruce-living spiders: effect of spider interactions and bird predation. Oikos 40:226–233.

Heinrich, B. 1979. Foraging strategies of caterpillars, leaf damage and possible predator avoidance strategies. Oecologia 42:325–337.

Holmes, R. T., J. C. Schultz, and P. Nothnagle. 1979. Bird predation on forest insects: an exclosure experiment. Science 206:462–463.

Kingsland, S. 1982. The refractory model: the logistic curve and the history of population ecology. Quart. Rev. Biol. 57:29–52.

Lack, D. 1971. Ecological isolation in birds. Harvard Univ. Press, Cambridge, Massachusetts.

Lotka, A. J. 1925. Elements of physical biology. Williams and Wilkins, Baltimore, Maryland.

MacArthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology 39:599–619.

———. 1972. Geographical ecology. Harper and Row, New York, New York.

Maurer, B. A. 1983a. Overlap and competition in avian guilds. Am. Nat. 121:903–907.

———. 1983b. Sensitivity analysis of a simulation model of bird-insect interactions in a deciduous forest ecosystem. Pp. 277–287 *in* Analysis of ecological systems: state-of-the-art in ecological modelling (W. K. Lauenroth, G. V. Skogerboe, and M. Flug, eds.). Elsevier, Amsterdam, Netherlands.

Miller, R. S. 1967. Pattern and process in competition. Adv. Ecol. Resear. 4:1–74.

Minot, E. O. 1981. Effects of interspecific competition for food in breeding Blue and Great Tits. J. Anim. Ecol. 50:375–385.

Morse, D. H. 1976. Hostile encounters among spruce-woods warblers (*Dendroica,* Parulidae). Anim. Behav. 24:764–771.

———. 1980a. Behavioral mechanisms in ecology. Harvard Univ. Press, Cambridge, Massachusetts.

———. 1980b. Foraging and coexistence of spruce-woods warblers. Living Bird 18:7–25.

Noon, B. R. 1981. The distribution of an avian guild along a temperate elevational gradient: the importance and expression of competition. Ecol. Monogr. 51:105–124.

NUDDS, T. D. 1982. Ecological separation of grebes and coots: interspecific competition or microhabitat selection? Wilson Bull. 94:505–514.

ORIANS, G. H. AND M. F. WILLSON. 1964. Interspecific territories of birds. Ecology 45: 736–745.

OTVOS, I. S. 1979. The effects of insectivorous bird activities in forest ecosystems: an evaluation. Pp. 341–374 *in* The role of insectivorous birds in forest ecosystems (J. G. Dickson, R. N. Connor, R. R. Fleet, J. A. Jackson, and J. C. Kroll, eds.). Academic Press, New York, New York.

PERRINS, C. M. 1965. Population fluctuations and clutch-size in the Great Tit, *Parus major* L. J. Anim. Ecol. 34:601–647.

PETERMAN, R. L., W. C. CLARK, AND C. S. HOLLING. 1979. The dynamics of resilience: shifting stability domains in fish and insect systems. Pp. 321–341 *in* Population dynamics (R. M. Anderson, B. D. Turner, and L. R. Taylor, eds.). Blackwell Scientific Publications, London, England.

PIELOU, E. C. 1981. The usefulness of ecological models: a stock-taking. Quart. Rev. Biol. 56:17–31.

PIMM, S. L. 1978. An experimental approach to the effects of predictability on community structure. Am. Zool. 18:797–808.

RICE, J. 1978. Ecological relationships of two interspecifically territorial vireos. Ecology 59:526–538.

ROBINSON, S. K. 1981. Social interactions and ecological relations of Philadelphia and Red-eyed vireos in a New England forest. Condor 83:16–26.

ROSENBERG, K. V., R. D. OHMART, AND B. W. ANDERSON. 1982. Community organization of riparian breeding birds: response to an annual resource peak. Auk 99:260–274.

ROTENBERRY, J. T. AND J. A. WIENS. 1980a. Temporal variation in habitat structure and shrubsteppe bird dynamics. Oecologia 47:1–9.

——— AND ———. 1980b. Habitat structure, patchiness, and avian communities in North American steppe vegetation: a multivariate analysis. Ecology 61:1228–1250.

RUSTERHOLZ, K. A. 1981. Competition and the structure of an avian foraging guild. Am. Nat. 118:173–190.

SAETHER, B. E. 1983a. Habitat selection, foraging niches and horizontal spacing of Willow Warbler *Phylloscopus trochilus* and Chiffchaff *P. collybita* in an area of sympatry. Ibis 125:24–32.

———. 1983b. Mechanism of interspecific spacing out in a territorial system of the Chiffchaff *Phylloscopus collybita* and the Willow Warbler *P. trochilus*. Ornis Scand. 14:154–160.

SCHOENER, T. W. 1974. Resource partitioning in ecological communities. Science 185:27–39.

———. 1976. Alternatives to Lotka-Volterra competition: models of intermediate complexity. Theoret. Pop. Biol. 10:309–333.

———. 1982. The controversy over interspecific competition. Am. Sci. 70:586–595.

———. 1983. Field experiments on interspecific competition. Am. Nat. 122:240–285.

SHERRY, T. W. 1979. Competitive interactions and adaptive strategies of American Redstarts and Least Flycatchers in a northern hardwoods forest. Auk 96:265–283.

SIMBERLOFF, D. 1982. The status of competition theory in ecology. Ann. Zool. Fenn. 19: 241–253.

SOLOMON, M. E. AND D. M. GLEN. 1979. Prey density and rates of predation by tits (*Parus* spp.) on larvae of codling moth (*Cydia pomonella*) under bark. J. Appl. Ecol. 16:49–59.

Tinbergen, L. 1960. The natural control of insects in pinewoods. I. Factors influencing the intensity of predation by songbirds. Arch. Nèerlandaises Zool. 13:265–343.

Toft, C. A., D. L. Trauger, and H. W. Murdy. 1982. Tests for species interactions: breeding phenology and habitat use in subarctic ducks. Am. Nat. 120:586–613.

Wiens, J. A. 1976. Population responses to patchy environments. Ann. Rev. Ecol. Syst. 7:81–120.

———. 1977. On competition and variable environments. Am. Sci. 65:590–597.

———. 1982. On size ratios and sequences in ecological communities: are there no rules? Ann. Zool. Fenn. 19:297–308.

——— and J. T. Rotenberry. 1979. Diet niche relationships among North American grassland and shrubsteppe bird populations. Oecologia 42:253–292.

——— and ———. 1980. Patterns of morphology and ecology in grassland and shrub-steppe bird populations. Ecol. Monogr. 50:287–303.

——— and ———. 1981a. Habitat associations and community structure of birds in shrubsteppe environments. Ecol. Monogr. 51:21–41.

——— and ———. 1981b. Morphological size ratios and competition in ecological communities. Am. Nat. 117:591–599.

Williams, J. B. and G. O. Batzli. 1979a. Competition among bark-foraging birds in central Illinois: experimental evidence. Condor 81:122–132.

——— and ———. 1979b. Interference competition and niche shifts in the bark-foraging guild in central Illinois. Wilson Bull. 91:400–411.

Wolf, L. L. 1978. Aggressive social organization in nectarivorous birds. Am. Zool. 18: 765–778.

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NORTH AMERICAN BLUEBIRD SOCIETY RESEARCH GRANTS

The North American Bluebird Society announces the second annual grants-in-aid for ornithological research directed toward cavity nesting species of North America with emphasis on the genus *Sialia*. Presently three annual grants of single or multiple awards totalling $3,000.00 are awarded and include:

Bluebird Research Grant—Available to student, professional or individual researchers for a suitable research project focused on any of the three species of bluebird from the genus *Sialia*.

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Further guidelines and application materials are available upon request from **Theodore W. Gutzke,** Research Committee Chairman, P.O. Box 121, Kenmare, North Dakota 58746. **Completed applications must be received by 31 January 1985; decisions will be announced by 15 March 1985.**